The Relationship Between COLONY POPULATIONS and HONEY PRODUCTION As Affected by Honey Bee Stock Lines

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CONTENTS

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The Relationship Between COLONY POPULATIONS and HONEY PRODUCTION As Affected by Honey Bee Stock Lines

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Although strong colonies of honey bees (*Apis mellifera* L.) are recognized as being more productive, extensive rather than intensive colony management is generally stressed. Farrar (*4*)[1] showed the mathematical relationship between population and production, emphasizing that a larger population increases the honey production per bee. The basis for the advantage of the larger population over the smaller is the colony's influence on brood rearing. The ratio of sealed brood to colony population decreases as the population increases, with a highly significant negative correlation between the two factors (Farrar *3*). This means that the larger population will have relatively fewer bees engaged in the rearing of brood and a greater percentage available for field work, and thereby the production of honey per bee will be increased.

Honey production is affected by many factors. The nectar flow is as important as the population. Hambleton (*8*) showed that certain weather factors affect the nectar supply. Available honey plants, seasons, localities, soil fertility, and agricultural practices are all interrelated in their effect on the nectar flow. Agricultural practices include the differential cutting of fields of nectar-producing plants within a farming area and the use of certain fields for growing legume seed so that the plants can bloom for a longer period. The honey flow indicates the colony's capacity to utilize the nectar supply and is affected by population, race or strain of bees, incidence of disease, and management. Colonies and apiaries with the same nectar supply may vary considerably in the intensity of the honey flow. Individual colonies often produce several times the average for the apiary. This is evidence that differences in population have a much greater effect on honey production than do differences in the nature of the nectar supply.

This study was conducted at the Bee Culture Investigations Laboratory in Madison, Wis., during 1946–48 to determine the effect of various stock lines of honey bees on the relationship between colony populations and honey production. The results of this study are still useful in 1961.

[1] Italic numbers in parentheses refer to Literature Cited, p. 19.

COLONY DEVELOPMENT

Farrar (*3*, *4*) concluded that a colony will develop more slowly in proportion to its total strength as the population increases above 10,000 bees. Figure 1 shows that a colony of 10,000 bees may have approximately 85 percent as many cells of sealed brood as it has bees, and this percentage tends to decrease at the rate of 12 to 14 percent for each increase of 10,000 bees up to 60,000 bees. Where a colony contains less than 10,000 bees, the percentage decreases sharply.

Theoretical calculations of colony development are introduced to illustrate how an increase in either the longevity of the worker bees or the prolificness of the queen could increase the colony population and thereby improve its honey production. Theoretical changes in these increases were introduced to predict their effects on normal colony de-

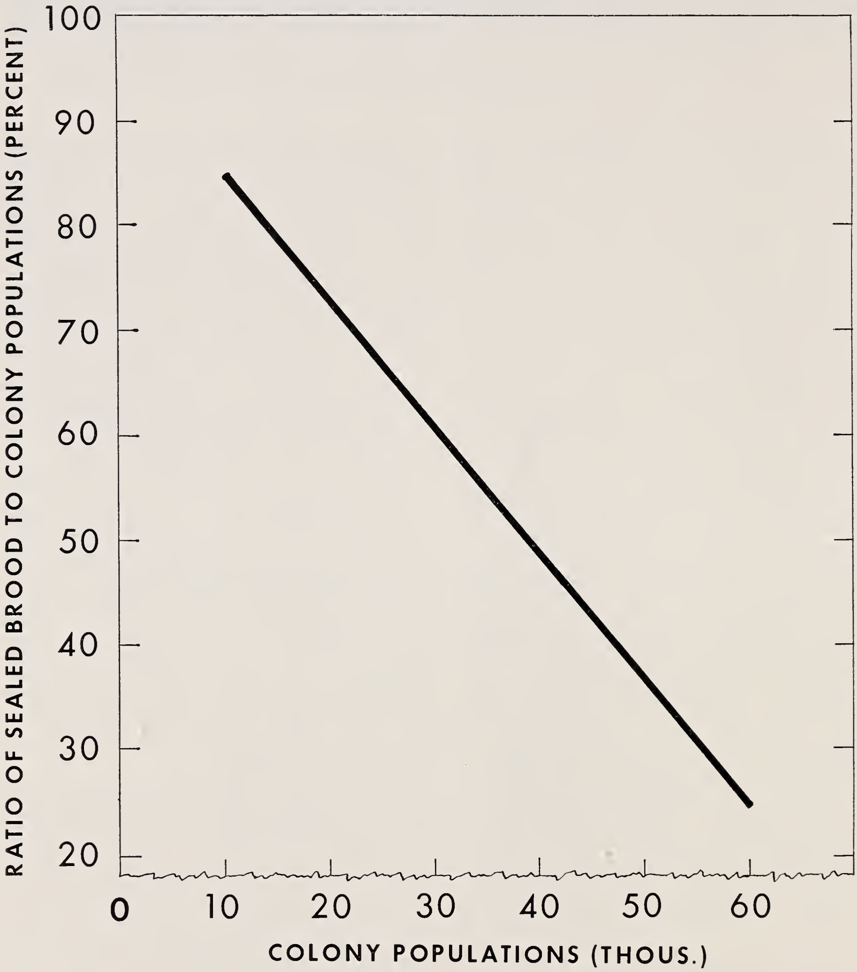

FIGURE 1.—Relationship between sealed brood and colony populations.

velopment. A normal colony is defined as a healthy colony working under optimum conditions. Diseases of brood or bees, abnormalities of the queen, swarming preparations, and abnormalities of environment, such as insecticide poisoning and unfavorable weather, were assumed to be absent. These calculations were applied to the basic relationship between brood and population observed by Farrar (*3, 4*) and illustrated in figure 1. A 2-pound package of honey bees installed on April 15 was used as the starting point for estimates of normal colony development. Farrar's brood-population data were used as a basis for normal colony development, and the theoretical population buildup was calculated. Average population and mortality rates over each 12-day period (time between sealing and emergence of brood) are shown in table 1.

The original 7,500 bees in the colony on April 15 (table 1) will all be dead by May 13. "Potential" bees include those in the colony plus those that will emerge in 12 days from the measured sealed brood. The "mortality" is the difference between the potential bees on one date and the actual number of bees 12 days later. The average longevity of bees at various population levels is theoretical, but the figures are representative of actual longevity values calculated from brood and population data.[2] Theoretical growth of the colony was terminated on September 2, since there is a normal reduction in all colony activities, including brood rearing, in the fall. It is evident from the calculations in table 1 that a package colony requires about 13 weeks to reach full strength.

According to Farrar (*5*) and Maurizio (*9*), many factors, such as Nosema, brood rearing, and pollen consumption, affect the longev-

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[2] MOELLER, F. E. THE EFFECT OF STOCK LINES UPON THE HONEY BEE POPULATION-PRODUCTION RELATIONSHIP. 1952. [Unpublished doctor's thesis. Copy on file Dept. of Ent., Univ. of Wis., Madison.]

TABLE 1.—*Theoretical development of a normal package colony of honey bees*

Date	Bees in colony	Sealed brood	Potential bees in 12 days	Mortality over 12-day period			Average longevity
				Days	Bees per day	Total bees	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Days*
Apr. 15	7, 500		7, 500				
May 5	2, 000±	6, 600	8, 600±				28
May 17	6, 600	6, 600	13, 200				28
May 29	13, 200	10, 250	23, 450				30
June 10	19, 050	14, 600	33, 650	8	550	4, 400	32
June 22	27, 050	17, 600	44, 650	12	550	6, 600	34
July 4	37, 326	19, 500	56, 826	4 6	550 854	7, 324	35
July 16	46, 834	19, 000	65, 834	6 4	854 1, 217	9, 992	35
July 28	53, 164	17, 850	71, 014	8 2	1, 217 1, 467	12, 670	35
Aug. 9	54, 719	17, 050	71, 769	10 1	1, 467 1, 625	16, 295	35
Aug. 21	52, 311	17, 850	70, 161	11 1	1, 625 1, 583	19, 458	35
Sept. 2	51, 260	18, 000	69, 260	11 1	1, 583 1, 488	18, 901	35

ity of bees. It is less affected by foraging activity, as implied by Phillips (*11*).

A comparison of the actual colony population with its potential population has shown marked differences in the average longevity of bees from different stock lines. The average longevity may vary by only a few days, but it can be decidedly important in determining the honey production of a stock line.

The effect of increased longevity on the colony population is illustrated in figure 2, where the maximum average longevity of worker bees was increased hypothetically

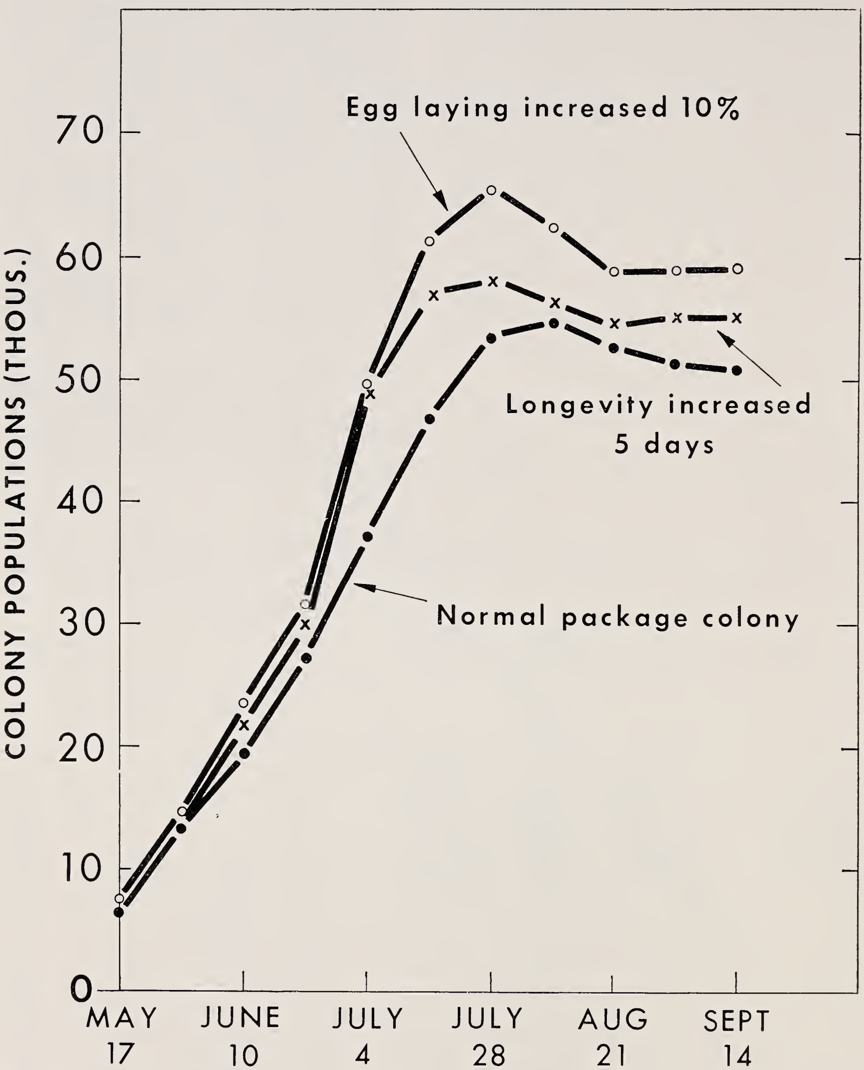

FIGURE 2.—Theoretical colony populations that would result if bee longevity could be increased by 5 days and the queen's egg-laying capacity could be increased by 10 percent as compared with the population of a normal package colony of honey bees.

from 35 days, as given in table 1, to 40 days. Similarly, variations in the queen's egg-laying capacity, which is largely responsible for the colony's growth, account for much of the variability between stock lines. The effect of increased prolificness of the queen on the colony population is also illustrated in figure 2. The theoretical populations reach their peak at about the same time as the population of a normal package colony. However, the populations attained will be greater when either the bee's longevity or the queen's prolificness is increased.

STOCK LINES

Eleven stock lines (commercial and experimental hybrids) were used in 1946, 7 in 1947, and 8 in 1948. In 1946 and 1947, 50 colonies were started from 2-pound packages of honey bees in late April, and in 1948 overwintered colonies were used.

In planning this study it was recognized that fewer stock lines would probably yield more significant data by providing more samples. However, fewer samples of a large number of stock lines were employed in an effort to measure differences in the available stock lines, since the testing-selection-breeding program had just been well started.

The hybrid lines were more uniform than the commercial stocks as to type of queen, prolificness, temperament of bees, propolization, swarming tendency, sealing of honey, and general behavior characteristics.

The stock lines used and their composition were as follows:

Stock line	*Composition*
	1946
S	Commercial
C	Do.
H	Do.
16A	16–3 × B149 × YF
17A	16–3 × B149 × H
21A	S10 × B149 × H
24A	S10 × 16–3 × YF
25A	S10 × 16–3 × H
26A	S118 × 16–3 × YF
27A	S118 × 16–3 × H
30A	A18 × W39 × W64
	1947
W	Commercial
S–9	YF × M4 × S
S–44	S (Madison '46) × S
60 and 60A	W64 × A18 × W39
61 and 61A	S10 × 16–3 × A18
62 and 62A	S10 × 16–3 × W39
63A	S10 × 16–3 × Caucasian
	1948
S–151–3	Commercial
107 × S	(D182 × B149 × Caucasian) × S
107A	(D182 × B149) × Caucasian
111A	(Caucasian × B149) × D182
123A	(W39 × W64) × A18
124A	(S10 × W39) × A18
126A	(S10 × W39) × Caucasian
127A	(S10 × W39) × (D182 × Caucasian)

Stock-line numbers followed by the letter "A" represent artificially inseminated test queens. The queens of stock lines 60, 61, and 62 were mated naturally under isolation to the same drone types as were used for 60A, 61A, and 62A. Other breeding data follow.

Stock line	*Developed from—*
A18	American foul brood-resistant stock
W39	Do.
W64	Do.
16–3	S commercial queens tested in 1940
S118	S commercial queen, colony 118, tested in 1943
S10	S commercial queen, colony 10, tested in 1944
D182	S commercial queen tested in colony 182 in 1946
B149	B commercial queen tested in colony 149 in 1942
M4	M commercial queen in 1945 but not tested
YF	Selected yellow queen mated to selected yellow drones from a 1945 cross of B149 × S118
Caucasian	Commercial Caucasian selection

These stock lines were at various stages of inbreeding during 1946–48. Many of the same stock lines were incorporated in hybrids tested from year to year, but no direct duplications of hybrids were made. Letter identification of commercial stocks was arbitrarily selected and does not refer to any particular commercial name.

METHODS OF COLLECTING DATA

Population Counts

Preparatory to measuring the colony population, the hive entrance was screened after dusk the previous night to prevent the field bees from leaving in the morning. The screen allowed clustering space outside the entrance and ventilation within the hive. Additional clustering space and bottom ventilation were given by inserting a ventilated rim between the bottom board and the first hive body. This rim was 4 inches high with a screened slit 2 inches high on both sides (fig. 3).

The next day the hive was weighed intact. The combs were then examined to find the marked queen. To prevent injury, the queen was caged and placed at the hive entrance. Then the bees were shaken and brushed from the combs and equipment into two empty hive bodies on the hive stand; the bodies were separated by a queen excluder. When nectar was present, the combs could be shaken lightly, but most of the bees had to be brushed from the combs. When free of bees, the combs were placed in weighed empty hive bodies and kept covered with a damp burlap sack. Damp cloths provide better control over robbing than wooden covers. Another damp sack was used to partially cover the two hive bodies into which the bees were shaken. This greatly reduced the flight of the bees and caused them to cluster. The occasional queen not found during these operations was invariably seen on the excluder and then caged. All the hive equipment was weighed to obtain the weight of the combs and the total weight of the hive without the bees. The difference between the weight of the intact hive with the bees and that of the hive without the bees was the weight of the bees. All operations were executed rapidly and systematically to shorten the period of disturbance and to avoid robbing.

A sample of 500 to 800 thoroughly mixed bees was taken from the bees clustered within the two hive bodies. These bees in the sample were anesthetized with hydrocyanic acid gas, weighed, and counted to get the average weight per bee. This weight was used to convert the total weight of bees into the number of bees. The sample of bees was then spread in front of the hive, where they recovered in about 15 to 20 minutes. Meanwhile, the hive was reassembled, all the bees were shaken down into the brood nest, the queen was released into the hive, and the supers and the cover were replaced.

The number of bees ranged from 6,160 to 10,560 per kilogram, or 2,800 to 4,800 per pound; the average was about 7,700 per kilogram, or 3,500 per pound. Differences in weight are dependent on the time of day, honey flow, temperament of the colony, and size of the bees. The amount of honey or nectar in the honey stomachs is affected by nectar flow and temperament, especially as regards the amount of smoke needed to subdue the bees. The size of the bees might be affected by the stock line and the age of the brood combs, the cells of which become smaller as more cocoons accumulate. However, in this study the stock line was responsible for differences in size, since all brood combs used were similar in age and condition.

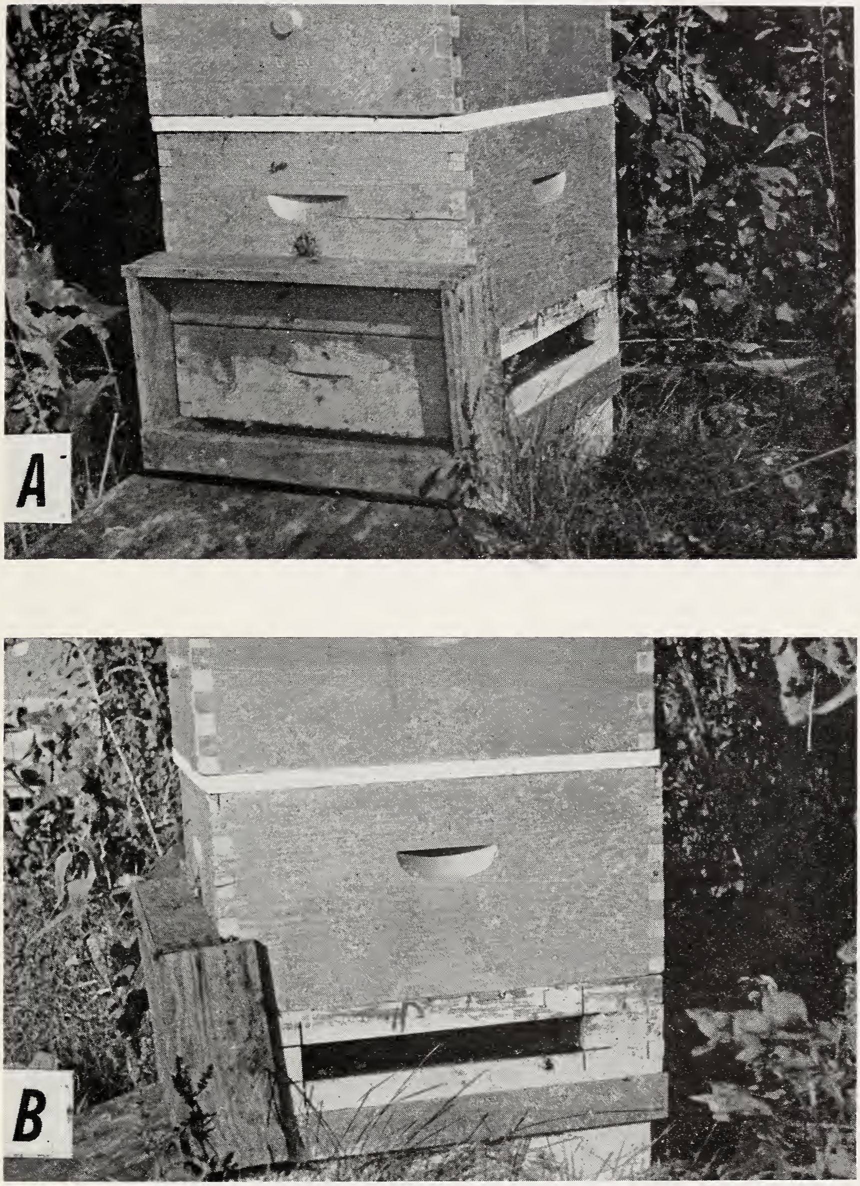

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FIGURE 3.—Front (*A*) and side (*B*) views of a hive, showing screened entrance and ventilated bottom rim.

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Over a 5-day week, population counts on all 50 colonies in the yard could be taken at the rate of 10 colonies per day.

Brood Measurement

The sealed-brood areas were measured on alternating weeks with the population counts in 1946 and 1947 and simultaneously with the population counts in 1948. The queen was caged for protection during this procedure. Each frame of brood was shaken free of bees, and a wire grid of 1-inch square mesh was placed over the face of the comb (fig. 4). Solid areas of sealed worker brood were counted directly, but partially filled areas or spotty brood was estimated. The number of square inches of sealed brood in the colony was multiplied by 25 to convert to the number of cells.

Limitation of Methods

Colonies subjected to population and brood measurements on a given day had little opportunity to forage on that day. To minimize this effect, the order of working the colonies was changed at each count.

The nectar flow varied considerably from day to day. The group of 10 colonies counted on one day was deprived of the nectar flow on that day, whereas the next group was deprived of the flow on some other day, often not of comparable intensity.

Occasional checks were made between the persons estimating the brood to avoid discrepancies, especially when the brood was patchy as in figure 4. Even one observer will change his estimated values because of fatigue. He thus needs to check his estimates frequently by actual counts.

Difficulties Encountered

During hot, humid periods confinement of strong colonies for a part of the day caused some suffocation of bees and resulted in probable injury and some mortality. This was overcome by using a top-moving screen over a hive body (fig. 5) and a ventilated rim at the bottom. In addition, the cover was partially raised or removed. Even then suffocation was observed occasionally in the last

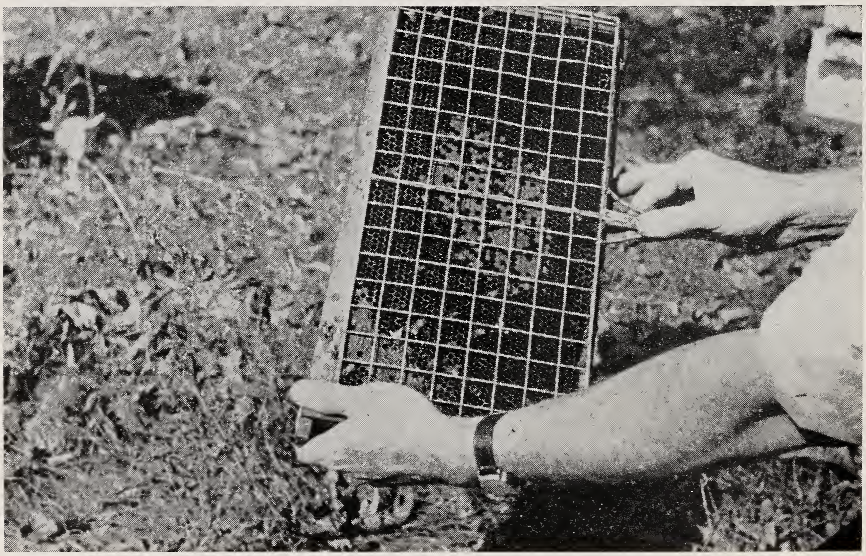

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FIGURE 4.—Counting sealed-brood areas.

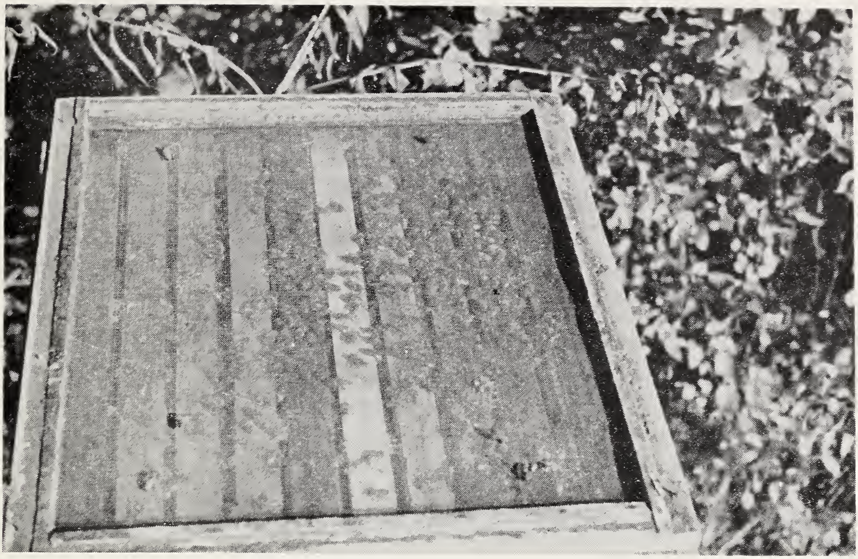

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FIGURE 5.—Top-moving screen over a hive body.

one or two colonies counted in the afternoon.

Certain hybrids were inclined to swarm more than others. The swarming tendency, in mild form, probably led to some queen supersedure. Colonies obviously preparing to swarm were omitted from this study.

An occasional queen was lost during manipulation, even though all queens were marked. When it was necessary to replace a queen, the colony was no longer used.

Each colony was so isolated by brush and trees that drifting of bees between colonies was minimized. During the shaking and brushing operations a moist burlap sack was used to provide a dark, cool clustering place for the dislodged bees. However, certain stock lines tended to fly more during the operation, and some drifting between colonies resulted. An effort was made to keep as few bees as possible from flying.

METHODS OF ANALYZING DATA

In Farrar's analysis of population-production data, individual colony populations were paired with honey production over the previous 2-week period. For this study the population at the beginning and that at the end of the 2-week period were averaged and this average was paired with the production value for the same period. Using this average offset differences in rate of colony development resulting from differences in brood emergence.

In comparing the regression trends of honey production on population for the various stock lines, it was sufficient to use the average of 2-week segments. A segment is any 2-week production period used to establish a point in a regression pattern. Since the study was carried through an entire season, all colonies were exposed to approximately the same nectar flow and the same treatment.

Regressions of production (Y) on

population (X) were calculated for all stock lines on every 2-week segment showing a gain period according to the following regression equation ($\hat{Y}$), in which x and y are the deviations from the averages of $X(\bar{x})$ and $Y(\bar{y})$, respectively, b is the regression coefficient, and n is the number of 2-week segments:

$$\hat{Y}=\bar{y}-b\bar{x}+bX$$

$$b=\frac{\Sigma XY-\frac{\Sigma X\Sigma Y}{n}}{\Sigma X^2-\frac{(\Sigma X)^2}{n}}$$

The correlation coefficient r was then calculated for each of these regressions according to the following equation:

$$r=\frac{\Sigma xy}{\sqrt{(\Sigma x^2)(\Sigma y^2)}}$$

The F values were also calculated for the 1947 data from an analysis of variance to check the significance of the regressions (Snedecor *14, pp. 244–250*).

The production period is not important in determining the relative production between colonies so long as it is constant for the group of colonies—2 weeks in this study. However, the production period should not be too long for this type of analysis, since smaller colonies make larger proportional gains in population because of their more intensive brood rearing (Farrar *3*), and their population-production level is thus raised within the production period. The available nectar supply and the opportunity for bees to collect nectar vary from day to day, depending on climatic and honey-plant conditions. Thus production values for the 2-week periods represent the total daily gains or losses of honey.

The effect of the stock line on production within the population range of the colonies was limited because of the small number of colonies and the narrow population range for each test group. To improve the accuracy of samplings within the environmental pattern, the regressions and correlations for each stock line were averaged.

The average regression within segments—hereafter referred to as average within regression—was based on the pooled sums of squares and cross products from within segments. The method of computing the average within regression is described by Snedecor (*14, pp. 400–401*).

Average correlation coefficients weighted as to the number of colony observations per segment were calculated according to the standard method (Snedecor *14, pp. 178–180*).

RESULTS

The averaged regressions and correlation coefficients for the different stock lines tested in 1946–48 are given in table 2. The heading "total colony observations" does not indicate the actual number of colonies observed but is the sum of observations within 2-week segments that showed production. For example, stock lines S in 1946 and W in 1947 were each represented by five colonies observed in two and four segments, respectively.

The individual 2-week segments for the stock lines tested in 1947 under good honey-flow conditions are given in table 3. Stock line S–44 had nine 2-week segments, because two groups of 10 colonies each were counted on alternate weeks.

TABLE 2.—*Relationship within segments between population* (X) *and honey production* (Y) *for several honey bee stock lines, Madison, Wis., 1946–48*

JUNE 10—JULY 10, 1946

Stock line	Total colony obser-vations	2-week seg-ments	Average within regression equation, $(\hat{Y})=$ Intercept	Regression coefficient	Degrees of free-dom for regres-sion	Average correla-tion coef-ficient (r)
	Number	*Number*				
S	10	2	+3. 1680	+0. 2638X	7	0. 0630
C	8	2	+2. 0309	+ . 3188X	5	. 4075
16A	2	1	−14. 3047	+ . 9203X	1	----------
17A	4	2	−9. 2095	+ . 4645X	1	----------
21A	6	2	−. 9903	+ . 2493X	3	. 4550
24A	8	2	+21. 4843	− . 3308X	5	−. 5915
25A	8	2	+14. 4342	− . 1539X	5	−. 3250
26A	4	2	−7. 9428	+ . 4404X	1	----------
27A	4	2	+6. 6825	− . 0227X	1	----------
30A	6	2	+15. 4942	− . 2272X	3	−. 6175
Total or average	60	19	+5. 6752	+ . 1064X	32	. 1180

JUNE 9—AUGUST 22, 1947

Stock line	Total colony obser-vations	2-week seg-ments	Intercept	Regression coefficient	Degrees of free-dom for regres-sion	Average correla-tion coef-ficient (r)
W	20	4	−8. 2354	+0. 5842X	15	0. 8485**
S-9	18	4	+21. 6130	− . 0236X	13	−. 0845
S-44	45	9	−7. 5563	+ . 6032X	35	. 4935**
60 and 60A	16	4	−3. 9961	+ . 6212X	11	. 6810**
61 and 61A	25	5	−. 4197	+ . 4204X	19	. 7275**
62 and 62A	20	4	−9. 3912	+ . 7905X	15	. 7940**
63A	30	5	−6. 3901	+ . 5306X	24	. 7270**
Total or average	174	35	−4. 6826	+ . 5388X	132	. 6425**

JUNE 14—JULY 30, 1948

Stock line	Total colony obser-vations	2-week seg-ments	Intercept	Regression coefficient	Degrees of free-dom for regres-sion	Average correla-tion coef-ficient (r)
S-151-3	11	3	−6. 4412	+0. 6645X	7	0. 7817**
107 X S	12	2	+48. 4724	− . 4395X	9	−. 3890
107A	4	2	+28. 5565	− . 1754X	1	----------
111A	10	2	+12. 9301	+ . 1928X	7	. 8710**
123A	10	2	−10. 7290	+ . 5341X	7	. 8345**
124A	4	2	+74. 7483	−1. 4485X	1	----------
126A	6	2	−4. 0686	+ . 6097X	3	. 7765
127A	8	2	+4. 5630	+ . 4330X	5	. 8260*
Total or average	65	17	+5. 7908	+ . 3176X	40	. 6680*

TABLE 3.—*Two-week segmental data showing relationship between population and honey production for several honey bee stock lines, Madison, Wis., 1947*

Stock line and number of colony observations per segment	Dates	Regression equation, $(\hat{Y})=$ Intercept	Regression equation, $(\hat{Y})=$ Regression coefficient	Correlation coefficient (r)	F reduction due to regression	Average population $(\bar{x})$	Average production $(\bar{y})$
						Thousands	*Kilograms*
W:							
5	June 24–July 8	−1. 2303	+0. 6441X	0. 8266	6. 4702	31. 30	18. 93
5	July 8–22	−21. 0696	+1. 0641X	. 9664**	42. 4023**	40. 40	21. 92
5	July 22–Aug. 5	−1. 6574	+ . 3237X	. 6277	1. 9516	45. 25	12. 99
5	Aug. 5–19	−7. 8365	+ . 3102X	. 6436	2. 1216	38. 77	4. 19
S-9:							
5	June 24–July 8	34. 8347	− . 1603X	−. 2351	. 1701	43. 51	27. 86
5	July 8–22	21. 7958	+ . 1334X	. 1676	. 1509	52. 88	28. 85
4	July 22–Aug. 5	−12. 7626	+ . 5218X	. 5451	. 8453	56. 54	16. 74
4	Aug. 5–19	75. 2584	−1. 4075X	−. 7535	2. 6266	50. 45	4. 25
S-44:							
8	June 23–July 7	6. 0108	+ . 4970X	. 5966	3. 3162	40. 26	26. 02
8	July 7–21	−12. 4785	+ . 8133X	. 6209	2. 6285	46. 50	25. 34
8	July 21–Aug. 4	−2. 3769	+ . 3759X	. 5150	1. 5935	46. 52	15. 11
7	Aug. 4–18	2. 7716	+ . 0629X	. 0878	. 0327	41. 31	5. 37
3	June 16–26	−34. 1673	+1. 2743X	. 8549	2. 7141	32. 40	7. 12
3	June 26–July 10	14. 3553	+ . 5470X	. 8758	3. 2929	36. 59	34. 37
2	July 10–24	14. 6773	+ . 1925X	------	------	40. 17	22. 41
3	July 24–Aug. 7	42. 1611	− . 6332X	−. 2618	. 0715	44. 49	13. 99
3	Aug. 7–21	−22. 0991	+ . 7553X	. 9160	10. 4238	37. 56	6. 27
60 and 60A:							
4	June 25–July 9	−38. 5365	+2. 1201X	. 9025	8. 7845	29. 28	23. 54
4	July 9–23	11. 9609	+ . 2810X	. 3458	. 2716	34. 73	21. 72
4	July 23–Aug. 6	14. 6981	− . 2526X	−. 3063	. 2070	35. 16	13. 81
4	Aug. 6–20	−38. 0770	+1. 4452X	. 8240	4. 2295	29. 89	5. 12

61 and 61A:						
5	June 16–26	−9. 8874+ . 5260X	. 7767	4. 5609	26. 63	4. 12
5	June 26–July 10	−7. 1216+1. 1163X	. 9118*	14. 7795*	31. 57	28. 12
5	July 10–24	8. 9361+ . 3471X	. 6460	2. 1484	37. 81	22. 06
5	July 24–Aug. 7	6. 4403+ . 1420X	. 3873	. 5296	41. 97	12. 40
5	Aug. 7–21	−6. 3273+ . 3032X	. 6448	2. 1349	37. 92	5. 17
62 and 62A:						
5	June 25–July 9	12. 9433+ . 3137X	. 3189	. 3397	30. 05	22. 37
5	July 9–23	−11. 4126+ . 9852X	. 9419*	23. 5937*	38. 34	26. 36
5	July 23–Aug. 6	−24. 7059+1. 0282X	. 9293*	19. 0010*	40. 99	17. 44
5	Aug. 6–20	−24. 9005+1. 0086X	. 5280	1. 1595	34. 94	10. 34
63A:						
6	June 16–27	−5. 4941+ . 4106X	. 7992	7. 0687	25. 29	4. 89
6	June 27–July 11	−8. 3569+ . 9637X	. 8383*	9. 4574*	33. 97	24. 38
6	July 11–25	−1. 2388+ . 4600X	. 4751	1. 1674	43. 78	18. 90
6	July 25–Aug. 8	26. 8852− . 2703X	−. 3442	3. 8325	48. 41	13. 80
6	Aug. 8–22	−12. 2066+ . 4997X	. 4975	1. 3155	44. 66	10. 11

DISCUSSION OF RESULTS

1946 Data

Seasonal conditions in 1946 resulted in essentially no honey flow. The average surplus from 290 test colonies, including the colonies in this study, was about 1 pound of honey for the entire season. The colonies gathered only sufficient nectar for them to replace the honey consumed in brood rearing. Colony populations developed normally and compared favorably with those in other years.

Individual colony data show that the colonies with the highest average populations were consuming honey at a faster rate than the smaller colonies, as was to be expected (Nolan *10*). However, had the nectar flow been of normal intensity, these colonies would have gathered the largest surplus because of their greater efficiency. None of the correlation coefficients were significant.

The nature of the honey flow was the main reason for the lack of correlation between population and honey production. The stock lines for the selected 2-week periods showed small production, because many of the days were spent consuming honey on account of inclement weather. Large colonies confined for many days consumed much more than smaller ones. Even though their production was considerably greater than that of the smaller colonies on flow days, the end result of a 2 weeks' observation made the smaller colonies appear the more efficient.

Further examination of the data shows discrepancies not easily explained. There was evidence that some of them were due to robbing, both from excitement caused during manipulation and systematic robbing of certain colonies in the yard. Systematic robbing is distinct from robbing as generally understood by beekeepers. In systematic robbing the bees are not nervous in their actions, but they proceed in an orderly fashion. The colony being robbed offers no resistance, and the bees apparently are unaware of what is taking place.

1947 Data

The honey flow was normal for the area in 1947. The data were the most complete of the three seasons. For these reasons information acquired during this year was most useful in analyzing the population-production relationship. Seven stock lines were represented, and six population counts were obtained from June 9 to August 22. On alternate weeks seven sealed-brood counts were made from May 19 to August 14. More efficient procedures were devised from experience obtained in 1946, and disturbances such as robbing were eliminated. A great divergence in relative production efficiency was exhibited between the various stock lines.

To check the significance of the regressions, Snedecor's F value was calculated from an analysis of variance (table 3). The correlation between honey production and population was significant in only 5 of the 35 periods. Some of the reasons for so few significant correlations include reduction in the number of colonies caused by queen supersedure, narrow population range, and differential orientation of colonies to different fields within the foraging area.

Regression for S–9 was not significant (table 2) because of the narrow population range between colonies in this stock line and because two segments had only five colonies and two segments only four colonies. If the data were plotted, the grouping would be centered at the narrow population range, with enough variability in production to skew the regression in any direction and result in nonsignificance.

The predicted production values for assumed populations from 20,000 to 60,000, based on the extended average regression for the seven stock lines tested in 1947, are shown in figure 6. Production at given population levels can be obtained by dividing colony gains by the number of bees indicated in any regression. The regressions for all stock lines except S–9 show an increase in production as colony populations increase. The average regression for the seven stock lines shows that the production rate for bees in colonies of 60,000 was 1.53 times that for bees in colonies of 20,000 (0.46:0.30). This fact emphasizes the greater efficiency of larger populations as compared with smaller ones. The positions of the different regression lines (fig. 6) indicate that the levels of production may be influenced by the stock line.

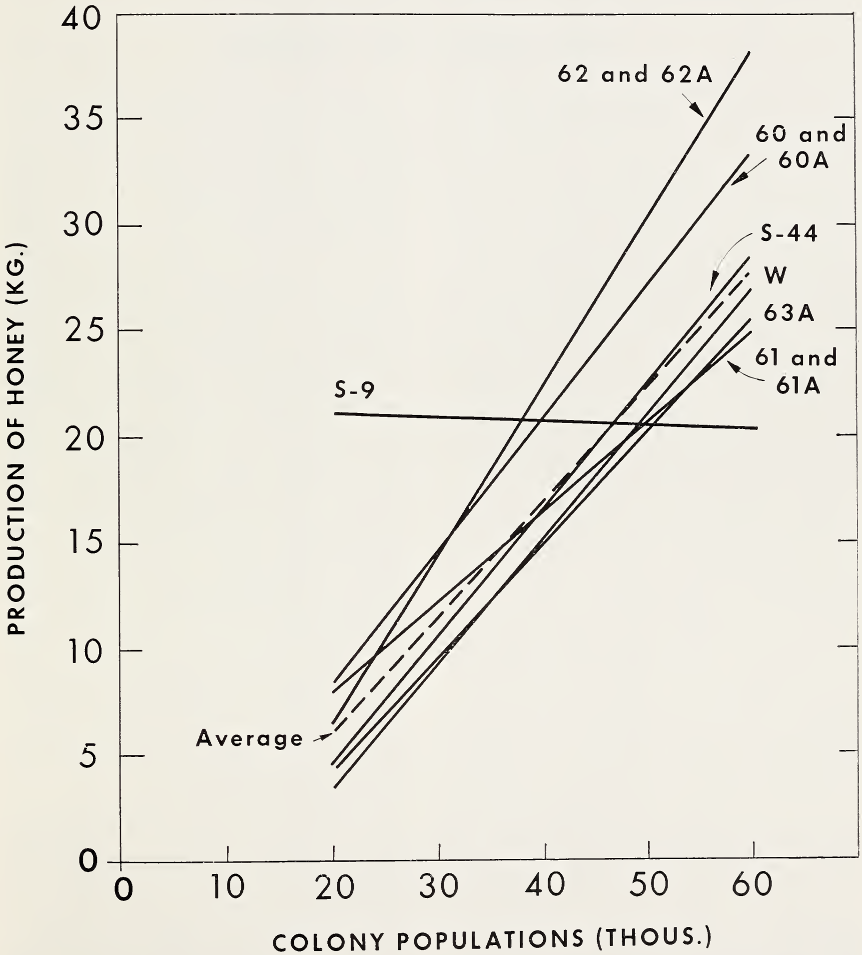

Figure 6.—Relationship between colony populations and honey production as affected by seven honey bee stock lines, 1947.

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1948 Data

The honey flow was again normal for the area in 1948. Four population counts from June 14 to July 30 were obtained on eight stock lines during the period of the main honey flow. The averaged regressions to enlarge the sample (table 2, 1948) contributed little, since there were only two segments. Only half of the correlations were statistically significant.

Failure to obtain significant data in 1948 on the population-production relationship indicates there were undetermined factors in operation. The apiary site had been cleared of brush, and new help was used in carrying out the required hive manipulations. Both the lack of brush for orientation of the bees to their hives and working with inexperienced help that lacked an understanding of bee behavior contributed to considerable drifting between colonies.

THE EFFECT OF LOCALE

In considering the significance of the statistical values one needs to recognize some of the complexities introduced by basic bee behavior. There is differential orientation among the colonies of an apiary foraging within a given area. The foraging area of one colony is often different from that of another. In this study tests were conducted in a diversified farming area, which did not necessarily provide all colonies with the same nectar supply. This factor may explain why correlations in this study were much lower than those reported by Farrar for Wyoming, where bee forage was not complicated by diversified farming.

A hypothesis is presented to explain the divergence from the expected relationship. The bee pasture available in Wisconsin resulting from diversified farming is in distinct contrast to that in Wyoming, where sweetclover and alfalfa are grown under irrigation and more than 8,000 acres of land are within flight range of an apiary. In Wisconsin this area would represent several hundred small fields varying in soil type, fertility, and moisture and on which are grown a great variety of crops, which are cut at different times. In Wyoming, where large acreages of excellent honey plants are allowed to bloom, there are more equal forage opportunities for all colonies.

Under the conditions present in Wisconsin, it is possible to have two colonies with similar populations in the same yard with greatly different production records if we assume the following pattern of bee activity: Colony A is working a field of alsike clover a mile to the north of the apiary. Colony B is working a similar field a mile to the east. If the clovers are allowed to go to seed, we might assume that each colony would produce approximately the same amount of honey. However, if the field to the north is cut for hay, colony A is temporarily deprived of its forage. It may be several days before this colony becomes reoriented to a new nectar source and resumes normal activity. Meanwhile, colony B is working uninterruptedly in the field to the east. We know that a colony can gain from 5 to 9 kilograms of honey a day during a good nectar flow. Hence, we can expect great differences in production between colonies of similar populations.

Package colonies 80X and 82 in 1947 illustrate such a situation. Both of these colonies of identical breeding (S10 × 16–3 × W39) had similar populations on four consecutive counts, as shown in table 4. The gain in weight of honey for each colony was essentially the same on the first, third, and fourth counts. However, on the second

Table 4.—*Population and weight of honey produced by two package colonies of honey bees (stock line 62A), Madison, Wis., 1947*

Date	Population		Loss or gain in weight of honey for—	
	Colony 80X	Colony 82	Colony 80X	Colony 82
	Number	*Number*	*Kilograms*	*Kilograms*
June 25	27, 276	23, 379	1. 07	−0. 63
July 9	30, 035	31, 593	26. 02	14. 15
July 23	39, 275	40, 668	23. 55	20. 43
Aug. 6	41, 178	39, 912	16. 21	14. 73

count the gain for colony 80X was 12 kilograms, or 25 pounds, more honey than for colony 82.

The validity of the proposed hypothesis is only a matter of conjecture. Further support of this hypothesis is found in the work of Butler (*1*), Von Frisch (*6, 7*), Ribbands (*12*), Singh (*13*), and Synge (*15*).

Butler (*1*), working with individual bees, showed that a honey bee does not generally wander at random over a crop of flowers but confines itself to a small area of the crop; the size of this foraging area is limited by the available food at the time. Singh (*13*) showed essentially this same fact.

Von Frisch (*6, 7*) in studies on the communication of bees showed how information about food sources discovered by foraging bees is transferred to other bees in a colony. The studies by Von Frisch make the theory of differential colony orientation seem plausible. For example, in his studies on training bees, he used honey to attract them. He had to wait many hours, often several days, until a bee finally would discover the feeding place. But as soon as one bee found the honey, many more, often several hundred, appeared within a short time. All the bees came from the same hive as the first bee, which indicated its discovery by means of the bee dances. This same principle of orientation of the bees of a single colony to an area can be applied to natural sources of floral nectar.

Ribbands (*12*), working with individual bees, reached similar conclusions as to their foraging habits and showed that sometimes a single flower may temporarily serve as the foraging area of one or more bees. Todd and Bishop (*16*), Eckert (*2*), Synge (*15*), and the author noted marked differences in pollens trapped from colonies. The greatest variation occurred when no major source of pollen was available and several plant species were in bloom at the same time.

The observations on pollen collection can be applied to the behavior of bees on nectar sources, since there is little reason to believe that the action of bees in nectar foraging should differ appreciably.

MODIFICATIONS OF METHODS AND TECHNIQUES FOR FUTURE WORK

Assuming the hypothesis that differential orientation of colonies is true, it is clear that the diversified agriculture of the Midwest presents a variable that cannot be changed. Measurements on larger numbers of colonies is the only way to reduce the effect of a variable nectar supply.

Uniform colony strength and

small numbers of colonies within stock lines, as encountered in this study, should be discouraged in any future work of this type. Since a comparison of different populations under the same nectar flow is the objective, each stock line should be represented by a minimum of 25 test colonies adjusted to give a wider range in population levels.

Since drifting of bees is a factor in shaking bees from the comb, every effort should be made to reduce drifting. In future work of this kind, a greater distance between colonies in a woodlot would be desirable. Rather than the 15- to 25-foot spacing used in this work, 100 feet would be preferred. The method of shaking bees so as to drop them where shaken rather than causing them to fly comes with experience.

To reduce the personal bias encountered in brood-area measurements, it would be desirable to have all such measurements made by one observer, and thus relative estimates would be given for each colony. The personal error could be further reduced by averaging the data of two observers estimating the same brood areas.

Although the manipulations were drastic, no adverse effect on colony performance was caused by the methods used. Since all colonies were handled in the same way, any such effect becomes a uniform variable.

SUMMARY

This study was undertaken at the Bee Culture Investigations Laboratory in Madison, Wis., during 1946–48 to determine the effect of various stock lines of honey bees (*Apis mellifera* L.) on the relationship between colony populations and honey production.

As established by Farrar in 1930 and 1937 and verified in this report, it is clear that production per bee increases as the population increases. The ratio of sealed brood to total bees in the colony decreases as the population increases, with a highly significant negative correlation between the two factors. This means that the larger population will have relatively more bees available for honey storage.

Stock differences in either the longevity of the worker bees or the prolificness of the queen could affect colony development and the production of honey. The effect of these variables was shown by calculating the theoretical populations obtained from a package colony at different levels of bee longevity and queen prolificness.

In this study population and production were determined every 2 weeks during the summer by weight. A sample of bees was weighed and counted to get the average weight per bee. This weight was used to convert the total weight of bees into the number of bees. Estimations of sealed-brood areas by means of 1-inch wire grids were made on all colonies on weeks alternating with the population counts in 1946 and 1947 and simultaneously in 1948.

All regressions and correlations in this study were averaged for each 2-week segment to obtain a greater number of colony observations. The 1947 data were the most representative of a normal season. The correlations, with one exception, were significant, ranging from 0.4935 to 0.8485.

The population-production data obtained during 1946–48 have a lower level of significance than was expected because of the small number of colonies used in most of the regressions or the very uniform colony strength within stock lines under unequal nectar resources.

A hypothesis was proposed to explain the apparent unequal nectar resources affecting the results. In

the Wisconsin area where this study was made, many crops are grown in small fields and are subjected to periodic cutting. A colony that is temporarily deprived of its main nectar source may be disrupted for several days until it reorients to a new field and resumes normal activity. Meanwhile, another colony of comparable strength might be working uninterruptedly on another field. Since we know that a colony can gain from 5 to 9 kilograms of honey a day during a good nectar flow, it can be seen that colonies with similar populations under these conditions could show great differences in honey production.

The data indicate that stock lines alter the population-production relationship. The comparatively narrow population range within small groups of colonies used in this study, together with the apparent variable nectar supply, gave many low correlations, yet the average regression between population and production was similar to that obtained in Wyoming (Farrar 1937). In future studies, each stock line should be represented by at least 25 test colonies adjusted to insure a wide range in populations.

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PRACTICAL INTERPRETATIONS

Within the normal colony the production per bee increases as the population increases. The beekeeper who operates full-strength colonies can produce several times more honey per colony than the beekeeper who operates at a lower level of efficiency with small colonies. Intensive management practices will give the highest return on his labor and investment.

Production of honey is a major criterion in selecting honey bee stock and breeding for improvement. A stock's productivity is affected by the number of eggs the queen lays, how long the bees live, the size or carrying capacity of their honey stomachs, their foraging behavior, and their susceptibility to disease.

Superior stock must be reasonably gentle and not prone to excessive swarming, maintain a compact heavy brood nest, and winter well. It should ripen its honey rapidly, cap the combs white, and use a minimum of bur comb. To obtain all the desirable characters in a superior stock, it is necessary to select and develop specific inbred lines from many sources and then recombine them into a genetically controlled hybrid. When this is done, hybrid vigor or heterosis usually results.

Well-reared queens of common stock that head well-managed colonies probably will be more productive than poorly-reared queens of superior stock. Likewise, well-reared queens of superior stock will require a higher standard of management than common stock.

To realize the maximum benefits from improved stock, the beekeeper must provide unrestricted room for brood rearing, ripening of nectar, and storage of honey. Although large colonies will use more pollen and honey in their development, they will frequently replace their food reserves from nectar flows that are not in evidence with inferior colonies.

The use of superior stock in hive equipment adapted to common stock may result in severe losses through swarming. The provision of food reserves adequate for common stock may result in starvation of superior stock; however, the superior stock, even though it consumes more honey, may be expected to produce a larger surplus than it consumes.

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